A QUAGGA, *EQUUS QUAGGA* (MAMMALIA, EQUIDAE), AT UNIVERSITY COLLEGE, LONDON AND A NOTE ON A SUPPOSED QUAGGA IN THE CITY MUSEUM, BRISTOL

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CONTENTS

SYNOPSIS

A mounted equid skeleton in the Department of Zoology, University College, London, is identified by its skull characters as *Equus quagga*, the extinct quagga of South Africa. An equid skull in the City Museum, Bristol, is not a quagga although accessioned as one.

INTRODUCTION

In the summer of 1972 I was asked to identify a mounted equid skeleton, Z581, in the museum of the Department of Zoology, University College, London. No written information existed about its history, but the number 41 had been written on the mandible a long time ago, and the late Professor D. M. S. Watson had once informed Dr K. A. Kermack that it was a quagga.

Z581 lacks canines and is therefore a female. It is adult; all the permanent cheek teeth are in wear and their occlusal surfaces much flattened. Infundibula, otherwise known as marks or central cavities, are still present in the upper and first lower incisors, so that the animal could have been 10–15 years old, were its ageing at all comparable with that of horses. Upper first premolars are present on both sides.

Z581 is not a horse, hemione or ass. Horse is ruled out by the relatively great width of the skull across the zygomatic arch compared with that across the orbits, the rather squared outline of the occipital in rear view, insufficient narrowing of the more dorsal part of the premaxilla, and deep V-shaped internal sulci of the lower molars. The zygomatic width and the normal instead of diminutive size of the occipital rule out the hemione. It cannot be an ass because of the great zygomatic width, insufficient narrowing of the premaxilla, the lack of any marked backward deflection of the top of the occipital in side-view, and the curved rather than the

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flattened lateral walls between the styles of the upper molars. There is no doubt that Z581 is a zebra, of which four species are known :

Grevy's zebra, *Equus grevyi* Oustalet, 1882, of parts of Somalia, eastern and southern Ethiopia and northern Kenya.

Mountain zebra, *E. zebra* Linnaeus, 1758, of the coastal region of the Cape Province of South Africa and southern South West Africa.

Burchell's zebra, *E. burchelli* Gray, 1824, with a range extending from the southern parts of the Sudan, Ethiopia and Somalia southwards to the Orange Free State and northernmost Cape Province.

Quagga, *E. quagga* Gmelin, 1788, an incompletely striped zebra formerly found in South Africa to the south of the Vaal River, in the Orange Free State and the southern Cape Province. It was heavily slaughtered in the 1850s and 1860s and became extinct in the 1870s. Specimens in European zoos survived until 1872 (London), 1875 (Berlin) and 12 August 1883 (Amsterdam). A number of specimens are available in museums, mostly as mounted skins, together with about a dozen skulls and five skeletons (Ridgeway, 1909 ; Hilzheimer, 1912 ; Rzasnicki, 1949 ; Lundholm, 1951 ; Willoughby, 1966 ; Rau, 1974).

COMPARISONS

The skull of Z581 was kindly lent to me for further study at the British Museum (Natural History). I established that it could not be a Grevy's zebra because it was too small, its face was short, and the premaxilla did not narrow in its upper parts. I then made a detailed comparison with up to 55 adult skulls of Burchell's zebra, 10 of mountain zebra and the museum's single example of a quagga skull, 1864.7.2.3, this last being from a complete skeleton of a male animal that lived in the London Zoo from 1858 until 1864 (Sclater, 1901). Its tooth wear is similar to Z581. The results of the comparison will be discussed character by character. The positions of all characters except the first are shown on a quagga skull in Fig. 1 and the skull of Z581 is illustrated in Plates 1–4.

1. The skull is smaller than in *Equus zebra*. Many *E. burchelli* approach it more closely, while the *E. quagga* skull is about the same size. It should be remembered that the quagga is a zoo specimen, that in the hemione and wild ass zoo specimens have skulls with linear measurements up to 10% smaller than their wild counterparts (Groves, 1966), that the same may be expected for zebras, and that Z581 may have been a zoo specimen itself. Thus the size of Z581 is appropriate for either *burchelli* or *quagga*. The back of M^3 is more posterior relative to the front of the orbit in Z581 and the *quagga* skull than in *zebra*, while *burchelli* is intermediate. Hence *E. quagga* and Z581 are rather short faced, but this character appears to be linked with overall skull size in living equids, and both the large Grevy's zebra and large domestic horses have long faces.

2. The interorbital area of the frontals shows a slight doming in *burchelli* but is flatter in *zebra*. The *quagga* skull and Z581 both resemble *zebra*. There is a

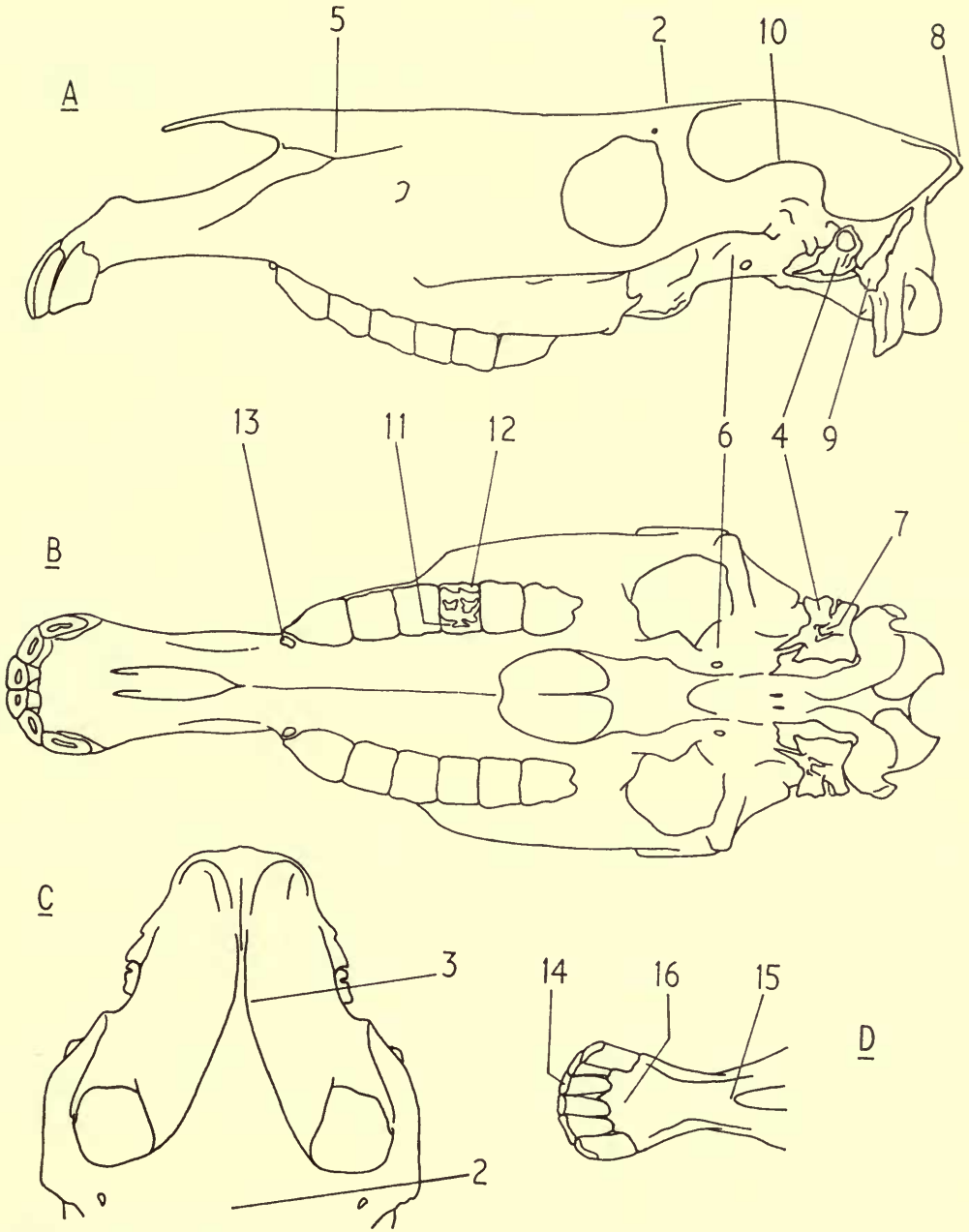

FIG. 1. Diagrams of a quagga skull to show the positions of characters 2 to 16, discussed in the text.

A. Lateral view.
B. Palatal view.
C. Dorsal view of postorbital part of skull.
D. Dorsal view of front of mandible.

possibility of regional variation within *burchelli* in that the doming seems less marked in specimens from South West Africa. Furthermore Dr D. A. Hooijer has told me that the *quagga* skull in the Leiden Museum shows a frontals' profile like *burchelli*. Nevertheless, Z581 would still lie beyond the *burchelli* range for the character, so that its affinities are with *quagga* or *zebra*.

3. The level of fusion of the two temporal lines to form a median sagittal line is more anterior in *burchelli* than in *zebra*. In 36 out of 50 *burchelli* it was forward of the rearmost level of the zygomatic arch in dorsal view ; in the remainder it was level or behind. In 2 *zebra* it was anterior, and in 8 level or behind. The *quagga* skull and Z581 have the fusion in the more posterior position, thus being unlike most *burchelli* but not unlike *zebra*.

4. The external auditory meatus is slanted upwards as it passes laterally in *burchelli* but emerges horizontally in *zebra* in which most individuals also have a larger meatal orifice. Both Z581 and the *quagga* skull resemble *burchelli*.

5. The maxilla-nasal suture dips anteriorly as it approaches the top of the premaxilla in both *zebra* and *burchelli*, but the phenomenon is more pronounced in *zebra* in which the top of the premaxilla suture is also more rounded so that a flange of the nasal bone descends a short way behind the premaxilla. Unfortunately the sutures become obliterated in older individuals. They are no longer visible with complete certainty in the *quagga* skull, but in Z581 they resemble the *burchelli* pattern.

6. The alisphenoid area on either side of the basisphenoid antero-medially to the articulation for the lower jaw is more nearly horizontal in ventral view in *zebra* than in *burchelli*. Z581 and the *quagga* skull are like *burchelli*.

7. *E. zebra* has a longer styloid process between the auditory bulla and the meatus than does *burchelli*. Z581 is like *burchelli* and the *quagga* like *zebra*.

8. In side-view the top of the occipital is drawn out posteriorly in *zebra*, but not nearly so much in Z581 or the *quagga*. Among the sample of *burchelli* 17 resemble *zebra*, 17 resemble Z581 and *quagga*, while 15 are intermediate and indeterminate. This character can also be seen in rear view as a relatively high occipital in *zebra* and a relatively low occipital in Z581 and the *quagga*.

9. The mastoid bone is wider in *zebra* than in Z581 or the *quagga* skull. In *burchelli* it is narrow in 37 and wide in 18 skulls. The flange of the squamosal between the mastoid and the external auditory meatus is also sometimes wide and sometimes slim, but may well be associated with the mastoid width. Of the 37 *burchelli* with narrow mastoids only 11 also have a slender squamosal flange, but among the 18 with wide mastoids 11 is again the number with a slender squamosal.

10. In *zebra*, the top edge of the zygomatic arch is fairly straight in lateral view and remains at more or less the same level. In the *quagga* and Z581 the top edge is more strongly curved and ascends posteriorly. Of the *burchelli* sample 27 skulls are like *zebra* and 25 like *quagga*.

11. On the upper molars the protocone or inner pillar is elongated anteriorly in 40 out of 50 *burchelli* individuals but not in *zebra*. The *quagga* skull and Z581 both resemble the majority of *burchelli*.

12. Cement is better developed around the exposed sides of the cheek teeth of *zebra* than of *burchelli*. A crude assessment of 'more' or 'less' cement showed that in only 9 among 48 *burchelli* skulls was there as much cement as in 7 out of 10 *zebra*. Both the *quagga* and Z581 skulls had 'more' cement and can be considered to be more like *zebra* than *burchelli*.

13. A small P^1 is present in 5 out of 10 *zebra*, these being mostly the younger individuals. It is present on at least one side in 30 of 51 *burchelli*, is often larger than in *zebra*, and there are indications that it is less frequent among the older individuals; it also seems to occur less often in *burchelli* from South West Africa. Erz (1964) believes that the tooth is part of the deciduous dentition. When present in *burchelli* it is often accompanied by a concavity in the front part of the medial wall of P^2. A relatively large deciduous P^1 is present in Z581, with only a slight concavity on P^2, but it is absent on the *quagga* skull. For this character Z581 thus resembles *burchelli* and differs from *quagga*, but the character must be very unimportant for classification.

14. Infundibula, marks or central cavities, are present in the lower incisors of *zebra* although less marked than those appearing in the uppers. This condition agrees with horses (Grossman, 1953 : 400). In old individuals the infundibula disappear from upper and lower incisors. However in *burchelli* infundibula were present in the lower incisors of only 6 among the 42 individuals in which they occurred in the upper incisors, and in 2 of the 6 they were present in I_1s alone. The London sample of *burchelli* again gives a hint of regional variation in that those from South West Africa appear to have lower incisor infundibula more frequently. In Z581 and the *quagga* skull infundibula were present in the upper incisors and I_1. This intermediate state may best be counted as a difference from both *zebra* and *burchelli*.

15. The posterior edge of the mandibular symphysis in the median line is high and more or less upright in *burchelli*. In *zebra* the top edge dips gently as it passes backwards and so curves round at a lower level to become the posterior edge. The height of the posterior edge is thus less than in *burchelli*. This character is difficult to assess except in sectioned mandibles, but is real enough as can be seen from Lundholm's illustration (1951, fig. 2). Both the *quagga* skull and Z581 resemble *burchelli*.

16. The top surface of the mandibular symphysis is noticeably flat behind the incisors in both the *quagga* skull and Z581. It could be linked with the incisors' occlusal surface appearing to be very little upturned. This character contrasts with most *burchelli* and *zebra*, even when the latter have very well worn teeth. It does not appear to be linked with a regression of bone around the incisor roots such as has taken place in both the *quagga* skull and Z581.

DISCUSSION

It seems from the 16 characters considered above that Z581 can be taken quite safely as *E. quagga*. The characters can be summarized as in Table 1, from which it is seen that Z581 differs from *zebra* in 13 of the 16 characters, from *burchelli* in 5 of the 16, but from *quagga* in only 2 of 15 characters, one of the two being the scarcely significant presence of P^1s. Accepting Z581 as *quagga*, one can suggest that skulls of *quagga* are like *burchelli* but differ in flatter frontals, a shorter united sagittal line on the cranial roof, more cement around the molars, better developed infundibula

TABLE 1

Summary of cranial characters

	Z581	*quagga*	*burchelli*	*zebra*
1. Size, smaller or larger	smaller	√	√	×
2. Frontals, convex or flat	flat	√	×	√
3. Level of fusion of temporal lines, anterior or posterior	posterior	√	×	√
4. External auditory meatus, slanted or horizontal	slanted	√	√	×
5. Nasal flange behind premaxilla, absent or present	absent	–	√	×
6. Plane of alisphenoid, slanted or horizontal	slanted	√	√	×
7. Styloid process, short or long	short	×	√	×
8. Occiput, drawn out posteriorly or more upright	more upright	√	intermediate	×
9. Mastoid, narrow or wide	narrow	√	√	×
10. Upper edge of zygomatic arch, curved and rising high or straight and low	curved, high	√	intermediate	×
11. Anterior part of protocone, elongated or short	elongated	√	√	×
12. Cement around cheek teeth, much or less	much	√	×	√
13. Deciduous P^1, present or absent	present	×	√	×
14. Infundibula of lower incisors, present or absent	in I_1s only	√	×	×
15. Shape of mandibular symphysis posteriorly, tall or low	tall	√	√	×
16. Surface behind lower incisors, flat or concave	flat	√	×	×

√ = agreement with Z581 ; × = difference from Z581 ; – = character not visible.

in the lower incisors and a flatter mandibular symphyseal surface behind the lower incisors. The poor extent to which the occipital top is drawn out backwardly and the strong curvature of the zygomatic arch are also characters which appear to be more distinctive of *quagga* than of *burchelli*. These findings are in agreement with the photographs of *quagga* skulls in Hilzheimer (1912, pl. 7, fig. 4, pl. 8, pl. 9, figs 3–4). The anterior elongation of the protocone is poorly developed in the Berlin skull A2617 of Hilzheimer, pl. 9, fig. 2, but this skull is not of a quagga (Antonius 1951 : 35).

Three other skull characters have been discussed in the past in relation to *quagga* but have not been used in the comparisons in this paper : diastema length, a preorbital cheek depression, and an upwardly bent profile of the anterior part of the nasals. Z581 has a longer diastema than the London *quagga* skull, as seen in the table of measurements, but the latter is unusual among quaggas, Hilzheimer (1912 : 100) giving much greater diastema lengths at 87, 97, 99 and 94 mm, as well as a juvenile at 55 mm. Lydekker (1904 : 428) observed the preorbital depression in the London *quagga* skull and took it as a differentiating character of the species, but similar vestigial depressions appear in some males of other zebras. There is no preorbital depression in Z581. The front part of the nasals is bent slightly upwards in the London *quagga* skull but not in Z581. Such an outline is present in about a third of the *burchelli* sample, although perhaps less frequent in specimens from South West Africa. Hilzheimer (1912 : 93) attributed the strength of this character in the London *quagga* skull to its having come from an animal which had been captive for a long period.

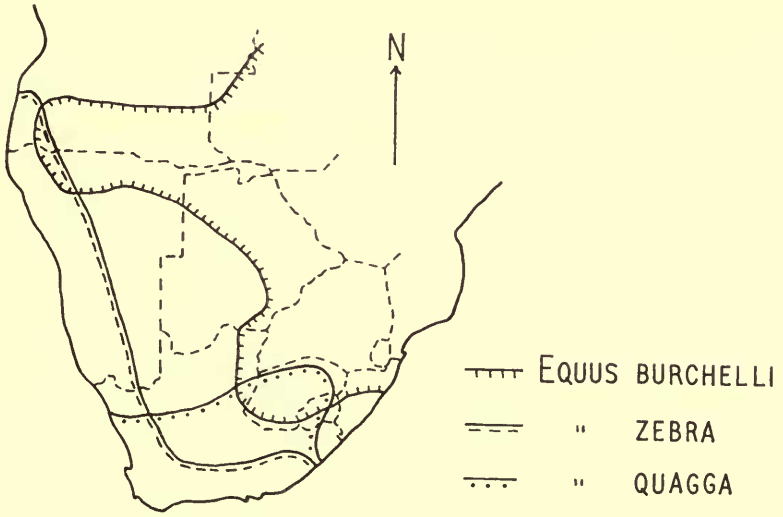

FIG. 2. Map of southern Africa to show the approximate original distributions of three zebra species. The original distributions of *E. quagga* and *E. zebra* are very uncertain, and their overlap may have been less than indicated here. Political boundaries are shown for guidance.

No known skulls of the extinct southernmost race of Burchell's zebra, *E. burchelli burchelli*, were available for use in the comparisons and it might be alleged that their skulls could have resembled *quagga* skulls more closely than do those of other *burchelli* races. As far as skin characters go, it is known that southern populations of *burchelli* tended to lose the posterior striping, and the beginnings of this trend can be seen even in surviving populations of *E. burchelli antiquorum*, the next southernmost race to *burchelli burchelli*. However, this resemblance to *quagga* may be more apparent than real; *quagga* had a brown body colour posteriorly, its posterior striping assumed a pattern unlike *burchelli* as can be seen on mounted skins in Tring and Vienna (Rau, 1974, figs 19, 21), it had no lighter 'shadow' stripes between the more posterior black stripes as seen in southern *burchelli*, and its dark stripes were wider relative to the white ones than in other zebras (also see Cabrera, 1936 : 91–2). It seems likely that both *zebra* and *quagga* were originally zebras of the more arid country lying to the south-west of the range of *burchelli* (Fig. 2), and that there is no need to suppose that skulls of *burchelli burchelli* would have approached those of *quagga* in their morphology.

A SUPPOSED QUAGGA SKULL IN THE CITY MUSEUM, BRISTOL

A male equid skull, Aa 3294, in the City Museum, Bristol, was accessioned in the latter half of 1927 and thought to be of a quagga. A pencilled note in the museum register reads : '? S. H. Swayne, 28 June 1872'.

I was able to see this skull on 24 January 1974, and it did not appear to be a quagga or any other species of zebra. It showed the following differences from zebras :

overall size is too small ;
skull width across the orbits exceeds that across the back of the zygomatic arch ;
premaxilla is narrow in side-view (even narrower than in Grevy's zebra), and narrows still more as it rises towards the nasal ;
occiput is rather small ;
braincase roof is too strongly curved in profile.

There are additional differences between the Bristol skull and the quagga skull in the British Museum (Natural History) :

the exposed part of the mastoid is too irregular in shape ;
vertical part of the rear median wall of the mandibular symphysis is too low ;
upper edge of zygomatic arch is insufficiently curved in side view ;
too little cement around the side walls and the cheek teeth ;
upper surface of the mandibular symphysis behind the incisors is more concave.

It is not necessary in this paper to provide an alternative identity for Aa 3294. However, its size and morphology agree well with two skulls in the British Museum (Natural History) of a Dartmoor pony and a Shetland pony. The rather small canines agree well with the Shetland pony, Osteology register 1952.4.1.3, and raise the possibility that Aa 3294 comes from a castrated domestic animal. The irregularly shaped mastoid is commoner in horses and ponies than in other equids.

TABLE 2

Measurements taken on the skulls discussed in this paper (mm)

	Equus quagga 1864.7.2.3	Z581	Aa 3294
Skull length, top of occipital crest to front premaxilla	494	482	431
Skull length, anterior edge foramen magnum to front premaxilla	446	442	398
Top of occipital crest to back of orbit	186	181	–
Back of orbit to front premaxilla	349	335	–
Skull width across posterior orbital rims	182	179	183
Skull width across zygomatic arch	174	178	177
Median length of nasals	–	194	171
Nasals breadth above infraorbital foramen	–	50·2	49
Occipital condyle to back M^3 at occlusal surface	209	208	174
Back M^3 at occlusal surface to front premaxilla	274	273	254
Diastema length, I^3 to $P^{I/2}$ (right side)	73·5	92	65
Occlusal length, M^1 to M^3	73	69·8	71
Occlusal length, $P^{I/2}$ to P^4	88·2	87·6	89

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REFERENCES

ANTONIUS, O. 1951. Die Tigerpferde; die Zebras. *Monographien der Wildsäugetiere* **11** : 1–124.

CABRERA, A. 1936. Subspecific and individual variation in the Burchell zebras. *J. Mammal.* **17** : 89–112.

ERZ, W. 1964. Tooth eruption and replacement in Burchell's zebra, *Equus burchelli* Gray 1825. *Arnoldia (Rhodesia)* **1**, 22 : 1–8.

GROSSMAN, J. D. 1953. *Sisson's Anatomy of Domestic Animals*, 4th edn. Philadelphia : Saunders. 972 pp.

GROVES, C. P. 1966. Skull-changes due to captivity in certain Equidae. *Z. Säugetierk.* **31** : 44–46.

HILZHEIMER, M. 1912. Die in Deutschland aufbewahrten Reste des Quaggas. *Abh. senckenb. naturforsch. Ges.* **31** : 83–105, pls 4–9.

LUNDHOLM, B. 1951. A skull of the true quagga (*Equus quagga*) in the collection of the Transvaal Museum. *S. Afr. J. Sci.* **47** : 307–312.

LYDEKKER, R. 1904. Note on the skull and markings of the quagga. *Proc. zool. Soc. Lond.* (1) : 426–431.

RAU, R. E. 1974. Revised list of the preserved material of the extinct Cape Colony quagga, *Equus quagga quagga* (Gmelin). *Ann. S. Afr. Mus.* **65** : 41–87, 25 figs.

RIDGEWAY, W. 1909. Contributions to the study of the Equidae ; ii. On hitherto unrecorded specimens of *Equus quagga*. *Proc. zool. Soc. Lond.* (2) : 563–586.

RZASNICKI, A. 1949. Complete list of the specimens of skeletons and skins of *Equus quagga quagga* (GM.) preserved in the museums of the whole world in 1939. *Annls Mus. zool. polon.* **14**, 5 : 69–73.

SCLATER, P. L. 1901. List of the specimens of the quagga that have lived in the Society's menagerie. *Proc. zool. Soc. Lond.* (1) : 165–166.

WILLOUGHBY, D. P. 1966. The vanished quagga. *Nat. Hist. N.Y.* **75**, 2 : 60–63.

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PLATE 1

Dorsal view of skull of *Equus quagga*, University College Z581. The scale in this and succeeding plates is marked in centimetres.

PLATE 2

Lateral view of same skull. The old number '41' is written on the mandible just above the number 'Z581'.


1.5.N
2.581

PLATE 3

Palatal view of same skull.

PLATE 4

A. Occipital view of same skull.
B. Occlusal view of lower dentition of same skull.


A
B